MATING BEHAVIOUR AND MATE CHOICE BY WILD AXIS DEER IN SRI LANKA[1]

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(With five plates)

During 20 months of field work in Wilpattu National Park (8°30′N, 80°1′E) in Sri Lanka I observed 24 complete sequences of mating in Axis deer (*Cervus axis*). I present here a description of 11 behavior patterns that constitute the sexual repertoire of the species. This I think will assist observers interested in all aspects of mating success and sexual selection in that polygynous species. I particularly make a distinction between mounting and inseminating, the latter being evident from the conspicuous thrust performed by the male. I also extend and confirm what others have shown, namely that most copulations (23 out of 24 in this study, and 61 out of 68, 90%, overall) are performed by the males in the largest antler-size class (about 75 cm or longer), even though they represent only some 30% of the adult males. Finally, I present some observations that strongly suggest that females can show an active preference for some males as mating partners.

INTRODUCTION

Among the repertoire of social behaviors of a species, mating behavior, i.e. courtship and copulation, is seldom fully and accurately described. This is certainly the case for wild mammals. In his excellent review of the subject, Dewsbury (1972) did stress the lack of extensive information on courtship and copulation of wild mammals in nature. Although the situation has improved since the publication of his seminal paper, only a few mammals, apart from primates, are adequately known (e.g. among wild ungulates: Geist 1971, 1981; Struhsaker 1967, Buechner & Schloeth 1965, Bützler 1974, Kurt 1968, Dubost 1971, Dubost & Feer 1981, Wemmer *et al.* 1983, Bergerud 1974, Bromley & Kitchen 1974, Lent 1974, Leuthold 1977, Walther 1984, Moss 1983).

Because they are rather stereotyped, courtship and copulatory behaviors are at once indicative of phylogeny (see Brown 1975), are very important for the reproductive isolation of species (an important theme in Mayr 1963) and may play an important role in female mate choice (see Bateson 1983). In addition, for the naturalist working under difficult field conditions, it may be of great use to know the full repertoire of courtship and mating. One can then infer with confidence from the incomplete observations often imposed by viewing distances or by forest habitats for instance, whether animals have actually mated. In the same way, once one knows the full sequence of events leading to copulation one can predict whether a courting pair that happens to get out of sight before copulation, will mate in that particular instance of courtship. In the case of forest animals this is particularly important. For instance, Markgren (1969), an authority on Moose (*Alces alces*) has written: "Successful mountings and completed coitus have rarely been observed. I have not seen one myself in seven years of field studies. This is unfortunate as this would be one way to determine the oestrus time of the cows ..."

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(Markgren 1969: 160) It is the main purpose of this paper to provide such necessary information on the Axis deer, or Chital (*Cervus axis*) living under natural conditions. Although Axis are locally numerous, and gregarious, thus relatively easy to observe, their mating behavior has only seldom been observed in their natural habitat, e.g. Schaller (1967) in his 14 month thorough and very inspiring study at Kanha in central India recorded only 2 copulations. In addition to describing the sexual behavior of Axis, I will use that information to discuss the intriguing subject of female mate choice, i.e. do larger males have privileged access to females only because they win in the intermale competition, or are they also preferred by the females as mating partners (see Bateson 1983 for a recent discussion of this important distinction initially made by Darwin 1871).

Study area and Method

I studied Axis in Wilpattu National Park (1300 km²) in Sri Lanka (8°30′N, 80°1′E) from September 1972 to October 1973, then again from April to October 1983, for a total of 20 months. Axis are numerous in the park, there were a minimum of 1000 of them (actual count on September 8, 1983) in the central part of the park where most observations were made. That study area is a 25 km² track of forest, interspersed with 12 rather permanent water holes (*villus*), each in the middle of a clearing whose diameter varies from about 200 m to 1 km (see Eisenberg & Lockhart 1972, for a description of the ecology of Wilpattu).

All observations were made from a vehicle that acted as a very efficient and convenient blind. Axis seemed to ignore the presence of the vehicle and they could thus be observed at close range without disturbance. Binoculars and a 20X telescope were used whenever necessary. The deer could be observed at almost any hour but were most active in the open from sunrise (around 0600) to about 1000, and from 1600 to sunset (around 1830). Observations were dictated to a field assistant who wrote down in coded form the behaviors as they occurred.

Results and Discussion

I have observed 24 full sequences of mating, 16 in 1973 and 8 in 1983. These include only cases where an ejaculatory thrust (see later) was actually seen. Courtship behavior was observed almost daily, in any month, with no obvious seasonal pattern. This is consistent with the fact that in Sri Lanka, Axis fawns can be born in any month (Phillips 1935, Eisenberg & Lockhart 1972, Barrette in prep.). In most instances of courtship, males performed only the first 3 or 4 patterns described here. The frequency of production of sexual behavior patterns by males of various antler-size classes in Wilpattu is very similar to what Schaller (1967) has reported for Kanha in central India. I therefore will not deal with that here. I will only give a description of the 11 patterns (10 illustrated with photographs) that constitute a complete sequence of courtship and mating. Some of them have been described by Schaller (1967) and Fuchs (1977). Many of these patterns are of course common to most Artiodactyls as well, as can be seen in the references cited in the introduction (e.g. Walther 1984).

1. *Low stretch.* This is an unambiguous sexual approach (Plate I, Fig. 1). The male's nose is pointed forward and his neck is held at or near the horizontal. Thus his antlers are laid back; i.e. relatively hidden from the female. The male usually flicks his tongue

rapidly as if licking in vacuo, and his penis is unsheated and pulsating more or less vigorously in the sagittal plane, both up and down, and in and out. The rythmic movement is thus not passively produced by the walking movements of the male. That action of the penis is very common in courting males, and is usually present at the merest approach toward a female, whether in the low stretch posture or not. It is so conspicuous that it may be a visual display. This is very different from the erection seen in violent fights. In the latter situation the penis is rigid and tucked against the animal's abdomen. The usual reaction of the female to a low stretch is to withdraw before being touched by the male, and she usually voids a few drops of urine while withdrawing (see Geist's 1981 discussion of that).

2. *Lipcurl* (*Flehmen*). After the female has withdrawn a few steps the male sniffs and/or licks the urine she left on the ground. Then raising his head in a posture very similar to the low stretch, the male stays motionless, except for an occasional slow and shallow vertical oscillation of the head. His upper lip is curled backward, his nares pinched almost completely, and his eyes partly or fully closed. The male stays in that transe-like posture for some 10 to 20 seconds, his muzzle pulsating as he breathes. He then lowers his head and actively licks his muzzle. Lipcurl apparently allows a male to assess the sexual receptivity of a female by sensing sexual hormones in her urine with the vomeronasal (or Jakobson) organ located above the roof of the mouth and connected to it through the incisive ducts (Dagg & Taub 1970, Estes 1972, Reinhardt 1983). As Geist (1981) has very aptly said, one of the primary purpose of courtship in Ungulates is to obtain urine from the female, in order to evaluate her degree of receptivity. In Chital, females lipcurl very seldom (I have seen it only once), fawns do it on occasion, like they playfully mount each other or adult females; velvet antlered males do it seldom, but hard antlered males lipcurl often. The performance of one lipcurl to the urine of a given female is usually a turning point in the courtship activity of a pair. In the vast majority of cases, lipcurl signals the end of courtship; a male presumably loses interest in a female once he has found out that she is not fully receptive (i.e. near oestrus). After such a lipcurl, a male ignores that given female and either approaches another one or grazes.

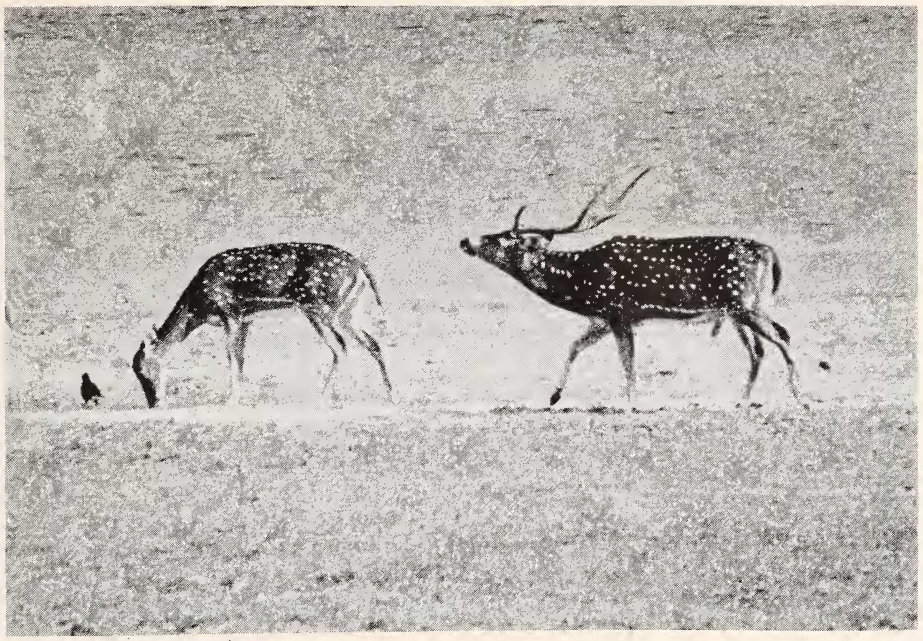
In addition to lipcurls performed during a social interaction, males are often seen to lipcurl by themselves, presumably to urine found on the ground.

3. *Guarding.* This is a very conspicuous behavior (Plate I, Fig. 2). The head is held high, the neck is stiff, the tail is stiff and strongly arched over the back, not merely vertical as in alarm behavior. Also the male marches in a stiff and exagerated manner, lifting his feet high and stamping them forcefully on the ground. The front feet are also occasionally stamped in place, as in alarm behavior. The male's penis is never visible during guarding. The male never grazes during a guarding episode, and never faces the female; he usually stays a few steps ahead of her, either parallel to her (Fig. 2), or blocking her way, he moves when she moves and stops when she stops. Whenever she drips urine, he picks it up and lipcurls, then resumes guarding. The best interpretation I can find for guarding is that the female is very close to oestrus, but not quite ready to be mated. This is supported by the fact that of all the instances of guarding I have seen (around 100), I have seen only twice a male mate with the female he was guarding. Thus guarding clearly indicates an intense interest in a female, but usually

does not immediately precede mating. Guarding is usually performed by the larger hard-antlered males (called big hards, i.e. males with antlers about 75 cm long or more). But guarding is not seen in all instances of courtship or mating, and it does not seem to be only a matter of the female's receptivity (see later in the section on mate choice). A guarding male is usually very persistent, and can guard non-stop for more than an hour. Occasionally however, a male seems to become impatient and will chase the female at a full run over hundreds of metres. Some of the chases are triggered by the female first trotting away from the male, but usually it is the male that does the first move, rushing one or two steps at the female with antlers pointing forward, and stamping both fore feet at once on the ground, the female then rushes off and the male chases her. As soon as she stops, he shops and resumes guarding. I do not agree with Schaller (1967:84) and Fuchs (1977:39) who call this posture a dominance or aggressive display. Although the guarding behavior is reminiscent of the "head-up display" of Schaller (1967:72), it is different in many aspects (the tail, the ears, the high stepping), and I never saw it performed among males. In addition, very often a male will perform his guarding in the absence of any other males, leaving no possibility of interpreting guarding as a form of inter-male aggressive display. Finally, a guarding male does not seem to attempt to herd a female either away from rivals, or back into the herd as some territorial bovids (Walther 1984), or harem forming cervids (Struhsaker 1967, Clutton-Brock *et al.* 1982) do. It seems that all that a male Chital tries to achieve is to advertize his presence and his persistence, by constantly monitoring, following and/or controlling the female's moves. If another male approaches however, a guarding male will occasionally lunge a few steps in his direction to have him withdraw.

4. *Licking vulva.* The first, and the most common, physical contact that a female Chital allows a courting male to do, is vulva licking (Plate II, Fig. 3). The female may move ahead at the instant of contact, or stand for many seconds and urinate (as on Fig. 3) while the male actively licks her vulva and drinks the urine. Either before, or immediately after, the female has moved ahead, the male usually lipcurls.

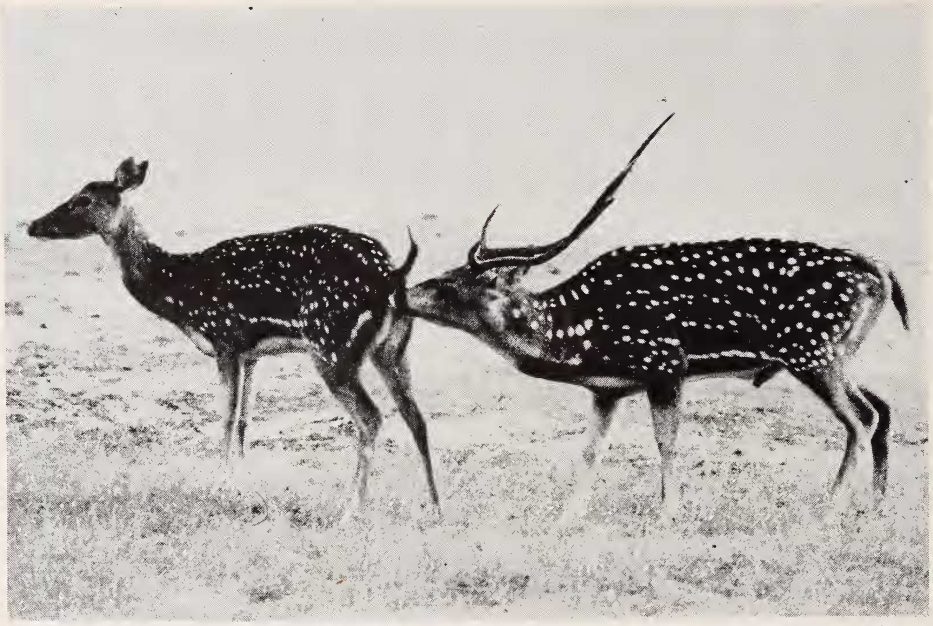
5. *Chin on rump.* If the female does not walk ahead during vulva licking, the male will eventually place his chin on her rump, flicking his tongue all the while, thus licking the female's rump. In the case illustrated (Plate II, Fig. 4), the female is standing, and holding her tail to the side. The male is about to rear (as evidenced by his lifted right fore leg) and mount. Almost all mounts (see later) are preceded by chin on rump, but in most cases, the female responds by moving ahead, with the male trailing her in low stretch, tongue flicking, licking vulva, chin on rump, and so on. This tending can go on for one hour or more before the female allows the male to mount, and in most observations, the animals get out of sight before it happens. When they do stay in sight for a long time, it very often happens that they do not mate at all even after a long tending period, the male eventually giving up, and grazing or resting. Thus chin on rump and the rest of tending are not reliable signs that mating is about to take place. Also, chin on rump is of course not a direct way for a male to restrain a female in order to mount her. It is more like a signal announcing the male's intention to mount. It is the female's response to that signal, i.e. walking or standing, that will result in the male mount-

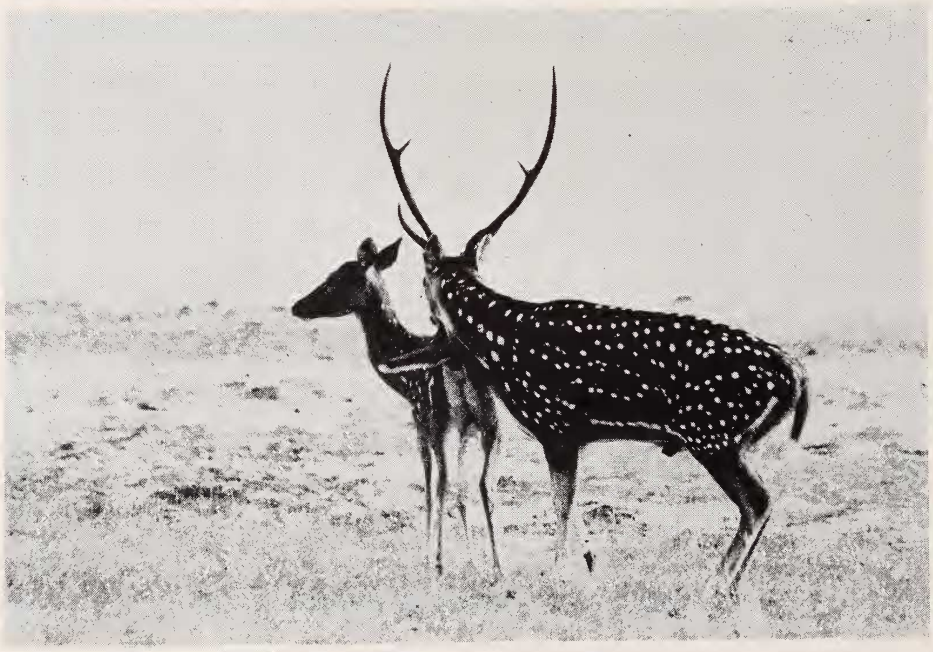


Above: Fig. 1. Low stretch. Note the difference in the tails, the female is probably dripping urine.

Below: Fig. 2. Guarding. A female that constantly holds her tail like here, has likely been bred not long ago.

(*Photos:* Author)





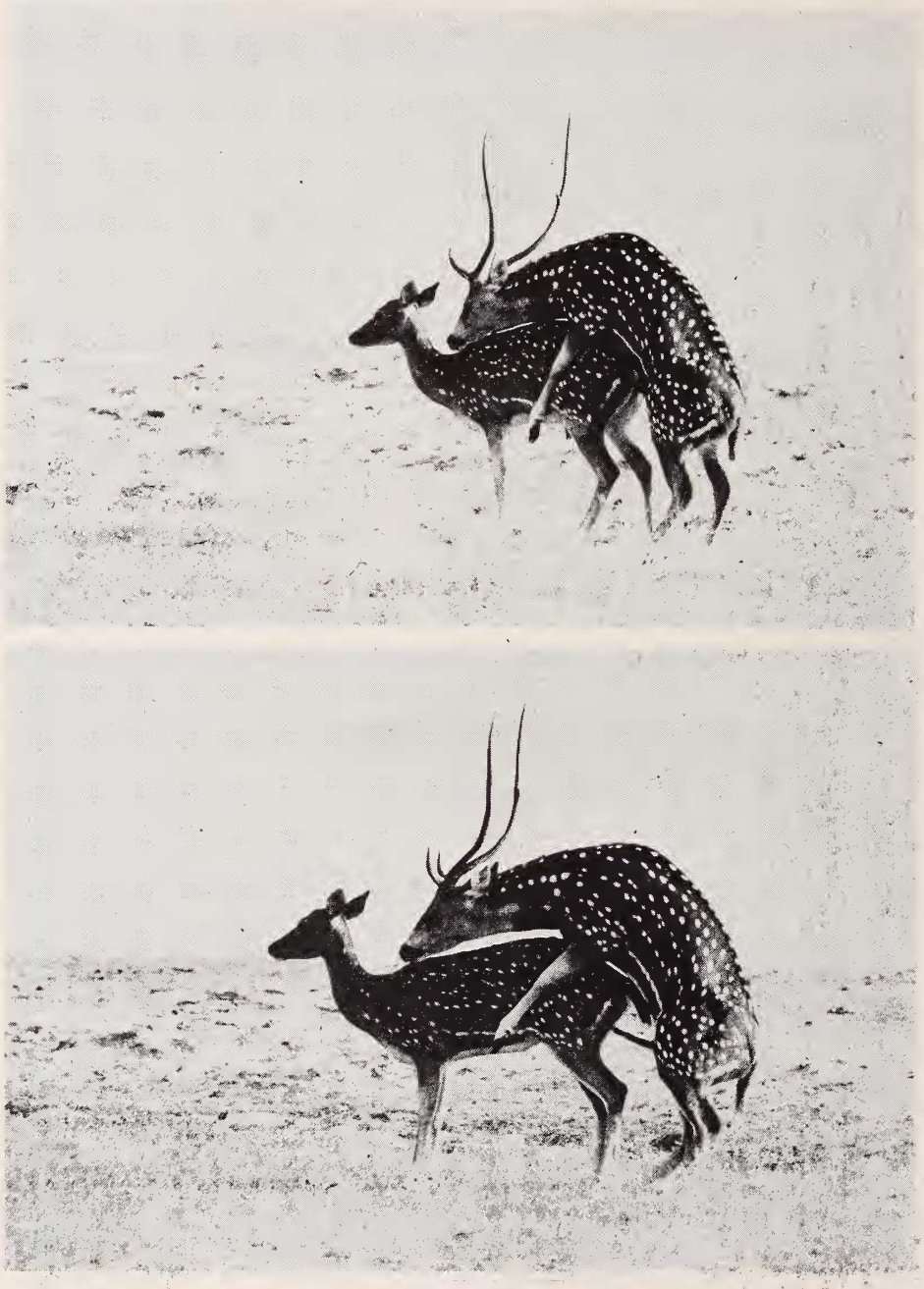
Abave: Fig. 3. Vulva licking. The female's arched back, raised tail and spread hind legs indicate that she is urinating. (Figures 3 to 10 incl. are from a single mating sequence).

Below: Fig. 4. Chin on rump. The female's tail is not wagging but held stiff and sideways.
(*Photos:* Author)

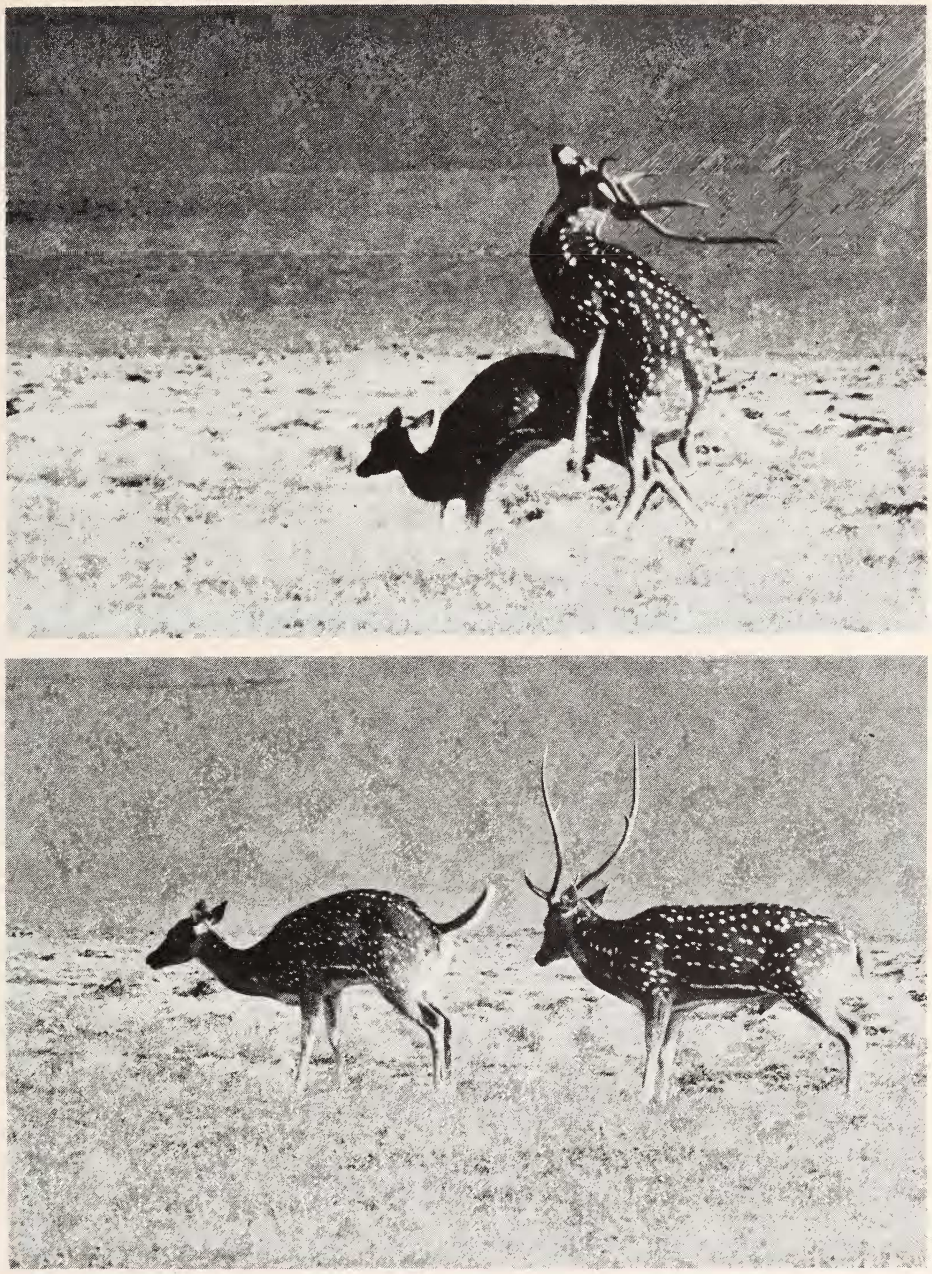
Above: Fig. 5. Chest licking. The male's tongue is visible. See how contorted he must be in order to lick the female's chest.

Below: Fig. 6. Attempted mount. The female is in the process of turning, just prior to stepping forward.

(*Photos:* Author)



Above: Fig. 7. Mount. The male is as far forward on the female as is possible.
Below: Fig. 8. Mount leading to intromission.
(*Photos:* Author)



Above: Fig. 9. Ejaculatory thrust. Note that the male's hind feet have moved adhead of the femal's, as compared to Figure 7. The female has fallen on her wrist joints. (This is taken from a colour slide).

Below: Fig. 10. Post copulatory postures.

(*Photos:* Author)

ing or not. Even though chin on rump cannot physically restrain the female, it may however function in a reflex manner as in suids, inducing a female to stop and stand firm (Signoret *et al.* 1975).

6. *Licking of the chest.* Chest licking is, as far as I could see, as sure a sign as any that mating is imminent. In this behavior, the male is beside the female and, twisting his head, he licks the ventral side of the lower neck, the chest, or even the inside of the fore leg on the opposite side (Plate III, Fig. 5). Whenever the female allows that form of contact, mating will take place within a few minutes. The male eventually stops licking, moves around the female, who stays put, places his chin on her rump and mounts. Out of 24 copulations I have seen in Wilpattu, chest licking occurred in 12 cases. I have seen chest licking only once without witnessing the subsequent copulation, and that was one case where the male was not a big hard (he was a medium hard; i.e. antlers between about 50 and 75 cm long), and where the pair entered the jungle while still courting. Chest licking never occurs at other times. This shows that a female that allows to be licked on the chest signals, to the male as well as to the observer, that she is ready to be mated now, and here.

It is worth noting that in Chital, mutual licking among adults is very rare. It occurs only during courtship. This is very different from some other cervids, most notably the muntjacs (*Muntiacus* sp.), where licking among adults is extremely common (Dubost 1971, Barrette 1977). In addition to vulva, rump, and chest licking by the male, female Chital occasionally lick a courting male's abdomen. This occurs only during an episode of mating, and it may be seen as a form of courtship on the part of a female.

7. *Attempted mount.* Rather often during a courtship sequence a female allows a male to go through the motion of mounting, only to slip forward before he can rest on her back (Plate III, Fig. 6). It often happens in such attempts that the two animals are not perfectly alligned (as on Fig. 6), this being usually a result of the female turning while the male rears behind her. It is usually as a result of the female stepping forward that a male dismounts. It does happen however that a male dismounts on his own from a female standing still, but only to immediately lick her vulva and mount again. A male usually does not walk in an attempt to remain upon a walking female, at the most he makes one or two steps before slipping down.

8. *Mount.* When the female stands perfectly still and the male is well in line behind her, he mounts by sliding his chin from her rump to her wither, flicking his tongue all the while (on Figure 7 his tongue is barely visible). This is different from an attempted mount, the male is far forward on the female, note the difference in the angle that the neck makes with the back compared to Figure 6. In Plate IV, Figure 7, it is a mount with attempted intromission. In any complete sequence of mating, a male mounts many times (mean and S.D. of 20 sequences accurately counted: 5.4 ± 3.1, range 2 to 16), ejaculating only once, on the last of those mounts (see later). The duration of mounts does not vary much, it is usually between 5 and 10 seconds, then the female either walks, more seldom, the male dismounts on his own (or ejaculates). The observation of mounting is not sufficient to conclude that mating is taking place. For one thing, yearling males with spike antlers occasionally mount females in a rather playful manner, and this has nothing to do with mating. Also, a male may go